THE SYSTEMATIC STATUS OF *AMBLYPHRYNUS INGERI* (AMPHIBIA: LEPTODACTYLIDAE) WITH THE DESCRIPTION OF AN ALLIED SPECIES IN WESTERN COLOMBIA

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SUMMARY

Amblyphrynus ingeri is known from three specimens, all collected on the Cordillera Oriental of Colombia. New material reveals that *Amblyphrynus* is inseparable from the *sulcatus* group of *Eleutherodactylus*. The *sulcatus* group contains five species: *E. helonotus, E. ingeri, E. maussi, E. sulcatus,* and a new species described herein on the basis of specimens from the Cordilleras Central and Occidental. The new species and *E. ingeri* are the most derived members of the species group and form a tight cluster with *E. sulcatus,* an Amazonian species.

RESUMEN

Amblyphrynus ingeri es una especie representada hasta ahora solamente por tres ejemplares, todos coleccionados en la Cordillera Oriental de Colombia. Nuevo material demuestra que *Amblyphrynus* es inseparable del grupo *sulcatus* de *Eleutherodactylus*. El grupo *sulcatus* contiene cinco especies: *E. helonotus, E. ingeri, E. maussi, E. sulcatus,* y una nueva especie que se describe en este trabajo con base en ejemplares provenientes de las Cordilleras Central y Occidental. La nueva especie y *E. ingeri* son los miembros más avanzados de este grupo de especies, y están estrechamente relacionadas con *E. sulcatus,* una especie amazónica.

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MATERIALS AND METHODS

Measurements and methods follow those employed by Lynch and Duellman (1980). Skulls were prepared by first picking away muscles and nerves. The cranium was then soaked in warm caustic (one part chlorox, three parts water) for 5 minutes followed by washing in cold water for 8-10 hours. Specimens are identified in the text by museum acronym and number as follows:

AMNH	American Museum of Natural History, New York.
BM	British Museum (Natural History), London.
FMNH	Field Museum of Natural History, Chicago.
ICN	Instituto Ciencias Naturales - Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá.
INDERENA	División de Parques Nacionales y Vida Silvestre, Instituto de Desarrollo de los Recursos Naturales, Bogotá.
KU	University of Kansas Museum of Natural History, Lawrence.
UMMZ	University of Michigan Museum of Zoology, Ann Arbor.
UV	Universidad del Valle, Cali.

Cochran and Goin (1961) named *Amblyphrynus ingeri* on the basis of a wellpreserved female taken on the eastern flank of the Cordillera Oriental in Departamento Cundinamarca. In 1970 they repeated their description in the Frogs of Colombia. Lynch's (1975) account of *A. ingeri* dealt chiefly with the juvenile frogs belonging to the new species described below. The discovery of two additional specimens of *Amblyphrynus ingeri* allows amplification of the details of the structure of this species and a reconsideration of its generic position. The newly discovered specimens are an adult male (ICN 4662) and a subadult female (ICN 2507).

The broad-headed eleutherodactyline frogs of Colombia have been rare frogs and their taxonomic history is one of indecision and error. The earliest report (Boulenger, 1882) was of a frog purportedly from Bogota which Boulenger identified as *Hylodes cornutus* (Jiménez de la Espada) in spite of several differences evident between the juvenile specimen and Jiménez de la Espada's (1871, 1875) description and illustrations. Peracca (1914) reported another example, again under the name *cornutus,* from Departamento Antioquia. Dunn (1944) reported the specimen which would ultimately be made the holotype of *Amblyphrynus ingeri.* Dunn's specimen, an adult female, was taken in the Cordillera Oriental, 8 km S Gachalá, San Isidro, Departamento de Cundinamarca. Cochran and Goin (1970) described and illustrated a specimen of *E. sulcatus* (Cope) in their account of "*Eleutherodactylus cornutus*" from Colombia. Lynch (1975) corrected a variety of errors, provided a historical resume of many of the errors and misidentifications, and contributed to the series of errors by assuming that several juvenile frogs from Andean Colombia were conspecific with the holotype of *Amblyphrynus ingeri.* He reported nine juveniles as *A. ingeri* and referred two other specimens (unseen: Peracca's frog from Camelia, Depto. Antioquia, and FMNH 69742, thought lost, from Valdivia, Depto. Antioquia) to that species.

Doctor Pedro M. Ruiz showed me two specimens of *A. ingeri* he collected in the Cordillera Oriental. I have also seen adults of another species from the Cordillera Central and C. Occidental. These western frogs are conspecific with all juveniles I previously reported as *A. ingeri,* and while closely related to *A. ingeri,* are clearly a distinct species. Doctor Ruiz generously permitted me to prepare skulls of each species. The skeletal data and the fresh material of *A. ingeri* allow a definitive statement of the relationships of this frog.

REDESCRIPTION OF *AMBLYPHRYNUS INGERI*

(Based on ICN 4662, adult male). Snout subovoid in dorsal view, sloping in lateral profile. Nostrils small, round, protuberant, directed laterally. Canthus rostralis moderately sharp, straight. Loreal region weakly concave, sloping gradually to lips; lips broadly flared. A frontoparietal furrow formed by cranial crests (low between eyes, but elevating posteromedial to orbits). Upper eyelid bearing one conical and several non-conical tubercles. Supratympanic fold prominent, extending from posterior edge of eye, above tympanum, then ventrad to above insertion of arm. Postrictal tubercles conical. Tympanum small, round, separated from eye by distance equal 1¾ tympanum diameters, elevated on side of head by inflated maxillary arch (Fig. 1).

Choanae small, round, not concealed by palatal shelf. Vomerine odontophores posterior to choanae, separated only slightly on midline, odontophores extending laterally to level of middle of choanae, bearing 9-10 teeth in feebly arched row. Palatine bearing an elevated ridge. Tongue longer than wide, fleshy, its posterior border not notched, posterior ¼ not adherent to floor of mouth. No vocal slits in male.

Skin of dorsum bearing numerous non-conical warts, least evident on head. An H-shaped series of ridges on occiput and anterior back. Posterior to the H are short paravertebral ridges and a second pair lateral to these (just anterior to sacrum). A pair of converging ridges lie above the coccyx. Warts on flanks larger than those of dorsum and several are elongate. Non-conical warts on upper surfaces of limbs but larger warts lie in the limb bands (forming ridges on shank). No anal sheath. Throat, venter, base of upper arm, and undersides of thighs coarsely areolate. Skin on ventral surfaces of shanks smooth.

Elongate, keel-like ulnar tubercles, scattered tubercles medial to ulnar keel on ventral surface of forearm. Palmar tubercle bifid, median lobe the larger. Thenar tubercle oval, much larger than palmar tubercle. Low supernumerary tubercles proximal to each subarticular tubercle. Basal subarticular tubercles large, longer than wide, non-conical; distal tubercles very small, round. Finger tips swollen but lacking discs. Lateral keels on fingers. First finger much longer than second. A white glandular nuptial pad on dorsal surface of thumb.

No tubercles on heel. Indistinct tubercles on outer edge of tarsus. A fold on distal ½ of tarsus (inner edge). Inner metatarsal tubercle 2½ times as long as wide, not compressed. Outer low, scarcely evident, round, ⅕ size of inner. Indistinct supernumerary plantar tubercles arranged in rows (metatarsals 2-4). Subarticular tubercles low, small, longer than wide. Toes bear lateral keels but no webbing. Toe tips expanded to form small pads, discs present on all toes, distal border sharply defined by circumferential groove, proximal border indefinite.

In preservative, brown above with black spots on posterior rami of scapular H and on anterior end of pre-sacral paravertebral ridges. A pale interocular bar. Head darker than body, reddish-brown. Supratympanic fold black, tympanum reddish-brown. Face brown with cream lines radiating from eye (defining labial bars). A reddish-brown canthal streak. Limbs rust brown with narrow bars (dark brown to black), slightly oblique. Throat brown with white flecks (tubercles). Venter white with some indistinct brown marbling. Underside of thighs like throat. Underside of shank brown laterally, cream medially, with two black bars distally. Groin and anterior and posterior surfaces of thighs brown with cream spots (edges poorly defined). Underside of tarsus and foot as well as forearm nearly black. Inner digits cream. Anal triangle gray-black.

Measurements of ICN 4662 and 2507 (♂ and ♀, respectively): SVL 32.1, 53.7; shank 16.3, 25.3; HW 16.65, 29.0; head length 12.1, 18.8; head length (chord) 15.2, 23.2; upper eyelid width 3.2, — —; IOD 4.0, 5.7; tympanum length 1.9, 2.6; eye length 3.8, 5.8; E-N 3.4, 4.5.

VARIATION. ICN 2507 is a young female with narrow although convoluted oviducts and ovarian eggs up to 2.6 mm in diameter. She is in poorer condition (somewhat desiccated and hardened) than the male and her skin is less tuberculate (warts more widely separated). Her cranial crests are larger than those of the male. Her vomerine odontophores bear 10 and 11 teeth and the choanae are oval (not round), slanted, and bordered by fleshy ridges. A distinctive suite of ridges are borne on the palatine bones (Fig. 2). Her snout is more sloped in lateral profile than that of the male.

The subadult female's cranium was removed to augment our knowledge of eleutherodactyline frog osteology. In the course of preparing the skull certain data were collected. The *depressor mandibulae* is in two slips, the posterior inserting on the fascia above the suprascapula and the anterior with fibers inserting on the otic ramus of the squamosal, tympanic annulus (posterior and ventral borders), and on the ascending ramus of the squamosal. Approximately 80% of the fibers inserted on the dorsal fascia. No *adductor mandibulae externus superficialis* was encountered. The mandibular ramus of the trigeminal nerve passes lateral to the *adductor mandibulae posterior subexternis.*

Skull (based on ICN 2507). The cranium is conspicuously flattened anteriorly and broader (28.65 mm) than long (premaxillae-occipital condyles 20.15 mm). Alary processes of premaxillae broad, directed posterodorsally. Septomaxillae large, lying just posterolateral to tips of alary processes. *Pars facialis* of maxillae deep, broadly contacting nasals, ornamented just anterior to orbit (and posteriorly). Maxillae deepening (as seen in profile) posteriorly, nearly reaching zygomatic ramus of squamosal. Posterior end of maxilla articulating dorsally with a sheet-like process from zygomatic and ascending rami of squamosal; ventral to this process is the greatly expanded quadratojugal. The infratemporal fenestrum is displaced posteriorly and is higher than long (Fig. 4).

The nasals are in median contact for their entire lengths, roughly triangular in outline, heavily ornamented, and slightly furrowed (along the midline) forming the vague cranial crests that extend onto the nasals (Fig. 2). The nasals and frontoparietals form a transverse suture (sphenethmoid entirely concealed). Frontoparietal fontanelles concealed. Frontoparietals heavily ornamented, bearing massive, broad crests along lateral margins. The crests are bony flanges bent laterally rather than solid ridges of bone. The lateral margins are irregular. Frontoparietals not fused to prootics. Occipital artery not enclosed in canal.

Epiotic eminences prominent. Cristae paroticae slender, broad, broadly overlapped by median extension of otic plate of squamosal. Squamosal crest ornamented (occupying all of otic ramus and most of zygomatic ramus of squamosal).

Occipital condyles ventrolateral to foramen magnum. Dorsal border of foramen magnum extended posteriorly by bone. Plectra long.

Palatal shelf of premaxilla relatively broad, deeply dissected. Palatal shelf of maxilla relatively narrow, broadening posteriorly. 9-10 premaxillary teeth (absent near midline); 52-55 maxillary teeth; 10-11 vomerine teeth. Vomers large, broadly in median contact, bearing arched odontophores; vomers bearing elevated flange along inner borders of choanae. Palatines broad, nearly reaching midline; lateral to vomerine odontophores, palatines bear long bony ridges (extending laterally nearly to maxillae). Cultriform process of parasphenoid sutured to vomers and palatines, broad, flat, bearing thickened lateral margins along posterior one-half of orbit. Parasphenoid alae oriented at right angles to cultriform process, broadly overlapped by median rami of pterygoids. Anterior rami of pterygoids not reaching palatines, forming broad suture with *pars facialis* and small pterygoid processes of maxillae.

In lateral view, frontoparietals meeting parasphenoid just anterior to optic foramen. Greatest height of skull (to top of cranial crests) 9.8 mm; to roof of frontoparietals 9.2 mm.

REMARKS. The new material reveals that *Amblyphrynus ingeri* has discs and small digital pads on the toes. As in *Eleutherodactylus sulcatus*, discs and pads are absent on the fingers. Lynch (1975) maintained generic recognition of *Amblyphrynus* because he thought discs to be absent in both species of the genus. Discs are also evident in fresh material of the new species (described below) but are not evident in the long-preserved material Lynch (1975) reported as juvenile *A. ingeri*. Tentatively, I consider the published claim that discs are absent in *A. helonotus* to also be incorrect; I suspect that fresh material will reveal the presence of discs on the toes of that species as well.

The osteological features of *A. ingeri* cannot be used to maintain recognition of the genus *Amblyphrynus* as distinct from the *sulcatus* group of *Eleutherodactylus;* accordingly, *Amblyphrynus* Cochran and Goin, 1961, is here placed in the synonymy of *Eleutherodactylus* Dumeril and Bibron, 1841. *Eleutherodactylus helonotus* (Lynch), new combination, and *E. ingeri* (Cochran and Goin), new combination, are members of the *sulcatus* group as defined by Lynch (1976).

THE NEW SPECIES FROM WESTERN COLOMBIA

The frogs reported by Boulenger (1882), Cochran and Goin (1970), Lynch (1975) and Peracca (1914) from the Cordillera Central, the Sierra Nevada de Santa Marta and from Bogota, are not conspecific with *E. ingeri* as suggested by Lynch (1975).

Eleutherodactylus ruizi sp. nov.

HOLOTYPE. Juvenile ♀, ICN 5211, obtained by John D. Lynch, 3 July 1979 (field number JDL 11128).

PARATYPES. ICN 4933, 4961-62, INDERENA (2, uncatalogued), KU 181992-93, UV 0001-2, topotypes. AMNH 39978-80, El Clara Creek, Depto. Antioquia, Colombia; AMNH 38639, 38649, Medellín, Depto. Antioquia, Colombia; FMNH 69742, Valdivia, Depto. Antioquia, Colombia; AMNH 104172, mountains above S side Lago de Calima (about 2 km airline SW village of Puente Tierra), Depto. Valle, Colombia, 1.580-1.600 m.

REFERRED SPECIMENS. BM 69.7.25.11, Bogotá, Depto. Cundinamarca, Colombia; MCZ 8237-38, Quindío mountains, Depto. Tolima, Colombia; MCZ 17577, west wide of Sierra Nevada de Santa Marta, Depto. Magdalena, Colombia.

TYPE-LOCALITY. Reserva Forestal de Yotoco, Km. 18, carretera Buga-Loboguerrero, Departamento Valle del Cauca, Colombia, 1.590 m.

ETYMOLOGY. The species is named for my colleague and friend doctor Pedro M. Ruiz-Carranza.

DIAGNOSIS. A species of the sulcatus group of *Eleutherodactylus* differing from all others in having a median growth of bone from the squamosal crest, fleshy ridges along the canthi rostrali, and an elongate tubercle on each eyelid (see Figs. 1, 3).

DESCRIPTION OF HOLOTYPE. Snout subovoid in dorsal view, slightly sloping in lateral profile. Nostrils small, oval, protuberant, directed laterally. Canthus rostralis sharp, accentuated by bony keel along canthus and fleshy fold extending anteriad from anterior corner of eye. Canthus straight (slightly concave immediately posterior to nostrils). Loreal region concave, sloping gradually to broadly flared lips. Large frontoparietal crests borne on lateral margins of frontoparietals (continuation of crests on nasals) extending to occiput and ending in slighly inturned boss. Skin between crests bearing ridges and subconical tubercles. Upper eyelid tuberculate; one elongate tubercle (length > 2 times basal width) near margin of eyelid; 4 smaller conical tubercles also on eyelid, some part of ridges. Crest of squamosal extending medially as flat raised area between eyes. Supratympanic fold extending behind tympanum; a second fold branches off of the supratympanic and extends along flank to about level of vertebra 5. Tympanum large, its annulus distinct except posterodorsally, higher than long, separated from eye by its own diameter (Fig. 1). Postrictal tubercles conical, but not especially prominent because other conical tubercles lie below eye.

Choanae longer than wide (teardrop-shaped, apex anterior), relatively large, not concealed by maxillary arch. Vomerine odontophores median and posterior to choanae, triangular in outline, separated on midline by distance equal to an odontophore width, bearing 5-6 teeth in a slightly slanted row (Fig. 3). Tongue large, as wide as long, feebly notched posteriorly, posterior edge not adherent to floor of mouth.

Skin of dorsum shagreened and bearing numerous subconical warts. A pair of folds extending from upper eyelid posteriorly to posterior level of suprascapulae. Posterior to these are a pair of paravertebral ridges and a pair of dorsolateral ridges (each terminate at level of sacrum). A pair of yet shorter ridges lie above the ilia. Skin of flanks like that of dorsum (bearing fold extending from supratympanic fold to about level of vertebra 5, then represented by conical warts to above groin). Skin of upper surface of limbs tuberculate; larger (conical) warts and short ridges accentuate limb bars. No anal sheath. A row of conical tubercles along margin of lower jaw. All ventral surfaces except concealed shank and tarsus areolate.

Three conical ulnar tubercles. Palmar tubercle bifid, inner lobe slightly larger than outer, each lobe smaller than oval thenar tubercle. Numerous supernumerary palmar tubercles, two on each metacarpal except outer (one). Subarticular tubercles large, round, non-conical (distal tubercles smaller than basal ones). Finger bear lateral keels. Tips of fingers slightly swollen but no discs present. Thumb much longer than second finger.

Heel and outer edge of tarsus bearing row of small conical tubercles. Fold (white) along inner edge of distal $2/3$ of tarsus. Underside of tarsus bears many round tubercles. Inner metatarsal tubercle $2\frac{1}{2}$ times as long as wide, not compressed; outer elongate, not elevated, $1/3$ size of inner. Numerous, distinct, supernumerary plantar tubercles, arranged in rows on all metatarsals. Subarticular tubercles longer than wide, subconical. Toes bear lateral keels but no webbing. Toe tips expanded to form small pads, discs present on all toes, distal border sharply defined, proximal border feebly defined.

In preservative, gray with black blotches associated with most ridges; ridges high-lighted with pale orange. Digits, especially medial, cream. Venter dirty white with brown marbling; throat brown with indefinite cream marbling. Underside of shank brown with cream and black spots. Underside of tarsus and forearm black with white warts and folds. Underside of thighs gray-black with dirty white spots. Labial bars black; a cream line from ventral edge of eye to rictus. Tympanum black.

In life, brown with rust wash above, some black spots on ridges; flanks creamy gray-white with brown reticulation. Venter gray-white with black reticulation. Posterior thighs gray with gray-cream and black spots. Iris brown above, gray below; flecked with gold.

Measurements of holotype. See Table 1.

VARIATION. The coloration and the arrangement of folds and tubercles on the skin are remarkably constant in the specimens examined. Preserved individuals vary from gray to brown in ground color. Sexual dimorphism is evident in the size of the tympana but is possibly also confounded by ontogentic change. UV 002 is a male 19.2 mm SVL; its tympanum length as a percentage of eye length is 64.8. AMNH 39980, another juvenile male (no vocal slits), is 20.6 mm; its tympanum/eye ratio is 84.3%. KU 181992, an adult male, 29.8 mm SVL has a tympanum/eye ratio of 85.7%. UV 001, an adult male, 38.9 mm SVL has a tympanum as large as the eye. This proportion for all females ($n = 9$) ranges from 54.3 to 74.4 percent ($\bar{x} = 66.2 \pm 4.8$). Means are presented as ± 2 standard errors. Other proportions (as percentages) are as follows: ♂♂ shank/SVL 44.8-51.9 ($\bar{x} = 48.9$, $n = 4$), HW/SVL 49.0-59.0 ($\bar{x} = 53.8$, $n = 4$), eyelid/IOD 75.0-120.0 ($\bar{x} = 91.6$, $n = 4$), E-N/eye 77.8-100.0 ($\bar{x} = 90.7$, $n = 3$); ♀♀ shank/SVL 47.6-54.5 ($\bar{x} = 49.9 \pm 1.8$, $n = 8$), HW/SVL 52.9-62.8 ($\bar{x} = 55.8 \pm 2.5$, $n = 9$), eyelid/IOD 68.3-95.8 ($\bar{x} = 82.9 \pm 6.5$, $n = 8$), E-N/eye 78.1-111.7 ($\bar{x} = 98.4 \pm 11.2$, $n = 6$). The difference in tympanum size is significant as is the difference in eyelid/IOD ratios. The means for the other ratios are not significantly different for sexes.

The skull was removed from ICN 4962. As in *E. ingeri*, the *depressor mandibulae* inserts on the dorsal fascia, otic ramus of the squamosal, tympanic annulus, and ascending ramus of the squamosal. No *adductor mandibulae externus superficialis* was found.

Skull (based on ICN 4962). The cranium is conspicuously flattened anteriorly and broader (29.5 mm) than long (premaxillae-occipital condyles 21.7 mm). Alary processes of premaxillae broad, directed posterodorsally. Septomaxillae large, lying just posterolateral to tips of alary processes. *Pars facialis* of maxillae deep, separated from nasals except above palatines, ornamented lateral to orbits and nasals. As seen in profile, maxilla not deepening but tapering only at posterior tip (Fig. 4). Quadratojugal expanded anteriorly, broadly articulating with maxilla.

The nasals are in median contact for their entire lengths, roughly triangular in outline, slightly ornamented (along crest), and bearing anterior extensions of cranial crests (Fig. 3). The nasals and frontoparietals form a transverse suture occluding the sphenethmoid. Frontoparietal fontanelles occluded by bone. Frontoparietals bearing tall, lateral crests ending posteriorly in inward-defleted flange (knob-like process reported for juveniles by Lynch, 1975). Frontoparietals feebly ornamented; not fused to prootic. Occipital artery enclosed in short canal on ventrolateral border of cranial crest (immediately above epiotic eminences).

Epiotic eminences prominent posteriorly; anteriorly they are indicated by bony flange. Cristae paroticae short, broad; functionally extended by median expansion of otic plate of squamosal. In dorsal view (Figs. 3, 5), these structures are concealed by a median extensiòn of the squamosal crest. The supraotic flange is heavily ornamented and extends farther medially than does the otic plate. Zygomatic ramus of squamosal bearing anteroventral extension of bone (irregular margins). Otic ramus of squamosal long.

Occipital condyles ventrolateral. Dorsal border of foramen magnum not extended. Plectra long.

Palatal shelf of premaxilla moderately broad, not deeply dissected; palatal process long. Palatal shelf of maxilla narrow, no pterygoid process. 9-11 premaxillary teeth; 56-58 maxillary teeth; 7-7 vomerine teeth. Teeth pedicellate. Vomers large, narrowly separated medially, odontophores triangular in outline. Palatines broad, extending medially to cultriform process of parasphenoid, bearing bony ridge. Cultriform process pointed, narrowly separated from palatines and vomers, not keeled, lacking lateral ridges. Parasphenoid alae oriented at right angles to cultriform process, broadly overlapped by median rami of pterygoids. Anterior rami of pterygoids not reaching palatines.

Frontoparietals not meeting parasphenoid on lateral wall of braincase. Greatest height of skull (to top of cranial crests) 11.6 mm; to roof of frontoparietals 9.6 mm.

DISCUSSION

The *sulcatus* group of *Eleutherodactylus* is now comprised of five species: *E. helonotus*, *E. ingeri*, *E. maussi*, *E. ruizi* and *E. sulcatus*. The new data necessitate a re-evaluation of my earlier remarks (Lynch, 1975) on the relationships among these species. All five species share the following derived character-states: areolate skin on venter, presence of lateral fringes on toes, flared lips and cranial crests. Other derived states are shared by two to four species: arched vomerine odontophores (all except *ruizi*); inner tarsal fold (all except *helonotus*); numerous pungent supernumerary plantar tubercles (*maussi, ruizi, sulcatus*); sloping snout (*ingeri, maussi, sulcatus*); cranial crests extending onto nasals (*ingeri, ruizi, sulcatus*); sphenethmoid not exposed-completely covered by frontoparietals and nasals (*ingeri, ruizi, sulcatus*);

elongate tubercle on upper eyelid *(ingeri, ruizi);* fleshy canthal folds *(helonotus, ruizi);* squamosals develop exostosed crests *(ingeri, ruizi).*

I lack data for *E. helonotus,* but the remaining species exhibit a graded series in terms of increasing depth of the posterior end of the maxilla (and adjacent quadratojugal) and growth of an anteroventral flange of the squamosal (Fig. 6). *Eleutherodactylus maussi* exhibits no enlargement of the maxillary arch and only a tiny anteroventral process (indicated by arrow, Fig. 6-A). *Eleutherodactylus sulcatus* has a moderately inflated maxillary arch and a larger anteroventral process on the squamosal (Fig. 6-B). The squamosal bears a very prominent process in *E. ruizi* (Fig. 6-C) and the maxillary arch is considerably inflated. In *E. ingeri* (Fig. 6-D) the maxillary arch is greatly inflated, nearly reaching the zygomatic ramus of the squamosal, and the squamosal bears a multilobed anteroventral process excluding the maxilla from the margin of the infratemporal fenestrum.

Another trait of interest (for which I lack data on *E. helonotus)* is the median growth of the otic plate. *Eleutherodactylus ingeri, E. ruizi* and *E. sulcatus* are identical in having an otic plate extending well onto the crista parotica whereas in *E. maussi,* the plate is less well developed (Fig. 7). The otic plate growth of *E. ruizi* is independent of the median growth of the otic crest (both are visible in Fig. 5). The otic plate of *E. maussi* is only slightly more extensive than that seen in *E. bufoniformis* (see fig. 99 in Lynch, 1971: 147).

The 10 characteristics (Table 2) can be used to construct a cladogram for the five species (Fig. 8) wherein *E. ingeri* and *E. ruizi* form a terminal branch and the pair in the sister group to the Amazonian *E. sulcatus. Eleutherodactylus helonotus* and *E. maussi* are less closely related although certain data are lacking for *E. helonotus.* The shape of the vomerine odontophores is not included in the cladogram. I suspect that broad arches are primitive to the group and that the state in *E. ruizi* (narrow, triangular odontophores) is paedomorphic and derived.

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TABLE 1

Measurements of six specimens of **Eleutherodactylus ruizi** sp. nov.

					Holótipo	
	UV	KU	ICN	KU	ICN	ICN
	0001	181993	4961	181992	5211	4962
	Ad. ♂	Ad. ♂	juv. ♀	juv. ♀	juv. ♀	young ♀
SVL	38.9	29.8	27.8	37.9	38.6	57.5
Shank	20.0	14.1	13.4	18.5	19.2	28.1
HW	20.7	16.1	15.4	21.6	20.9	30.4
HL	15.9	11.9	12.1	15.0	14.3	22.3
Upper eyelid	4.3	3.1	2.8	4.6	4.0	—
IOD	5.2	3.5	4.1	4.8	5.3	6.7
Tympanum	4.5	3.0	2.3	3.3	3.2	3.8
Eye	4.5	3.5	3.2	4.5	4.3	6.0
E-N	4.5	3.3	3.3	4.5	4.8	6.7

TABLE 2

Character-states for ten traits of frogs of *sulcatus* group. 0 = primitive states, 1 is derived, 2 is derived from state 1, 3 is derived from state 2, ? means data not available.

Characteristic	Species				
	helonotus	*maussi*	*sulcatus*	*ingeri*	*ruizi*
1. Tarsal fold	0	1	1	1	1
2. Supernumerary tubercles	0	1	1	0	1
3. Snout sloping	0	1	1	1	0
4. Cranial crests on nasals	0	0	1	1	1
5. Sphenethmoid concealed	0	0	1	1	1
6. Eyelid tubercles	0	0	0	1	1
7. Fleshy canthal folds	1	0	0	0	1
8. Squamosal crests	0	0	0	1	1
9. Squamosal-maxilla	?	0	1	3	2
10. Elongate otic plate	?	1	2	2	2

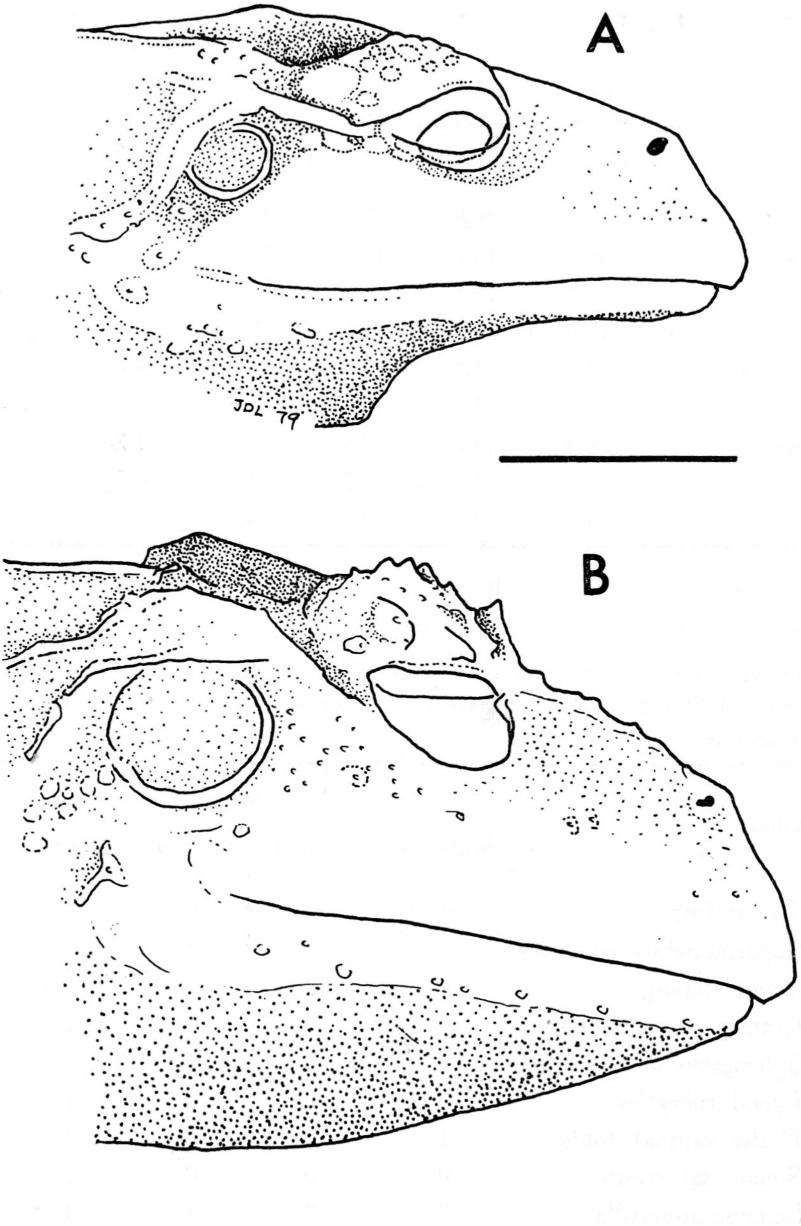

FIGURE 1. Profiles of *Eleutherodactylus ingeri* (A, ICN 4662) and *E. ruizi* sp. nov. (B, ICN 5211). Line equals 5 mm.

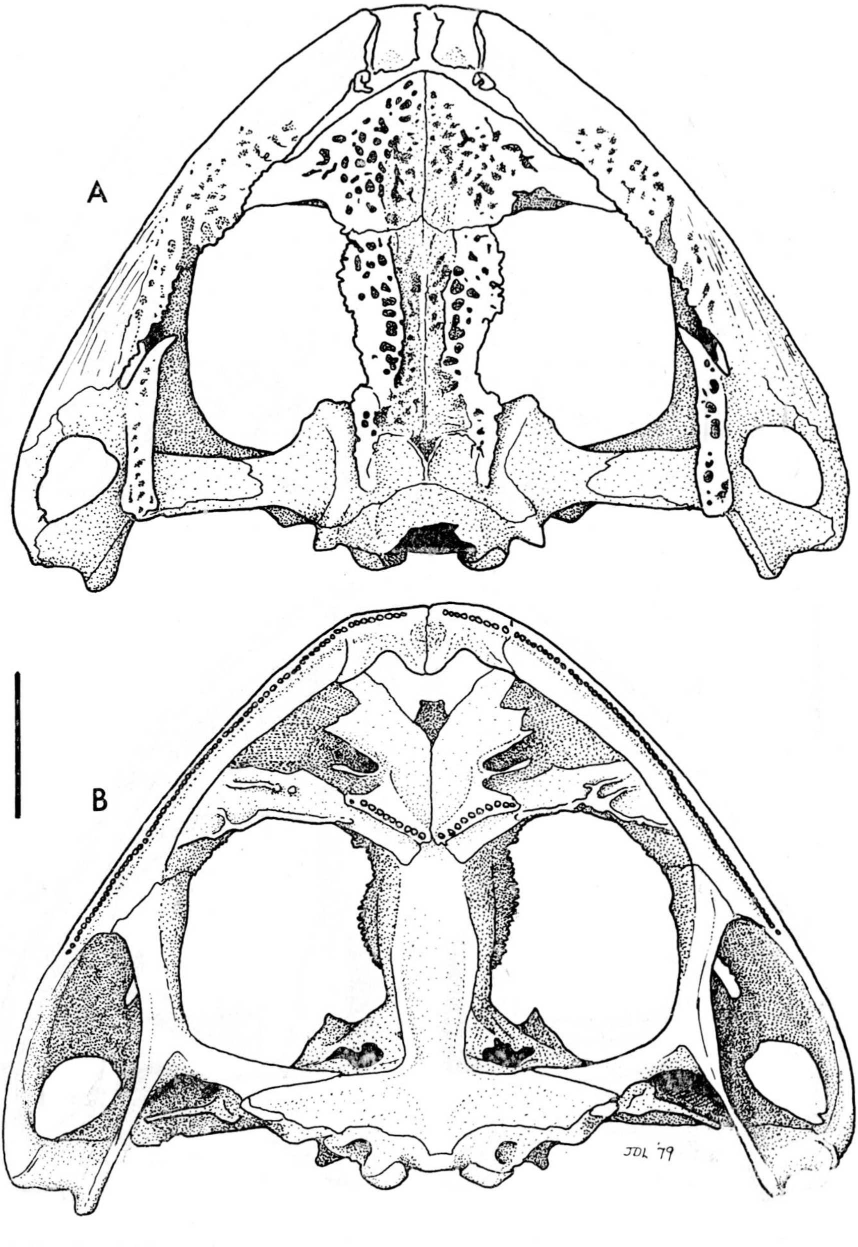

Figure 2. Skull of *Eleutherodactylus ingeri* (ICN 2507). Line equals 5 mm.

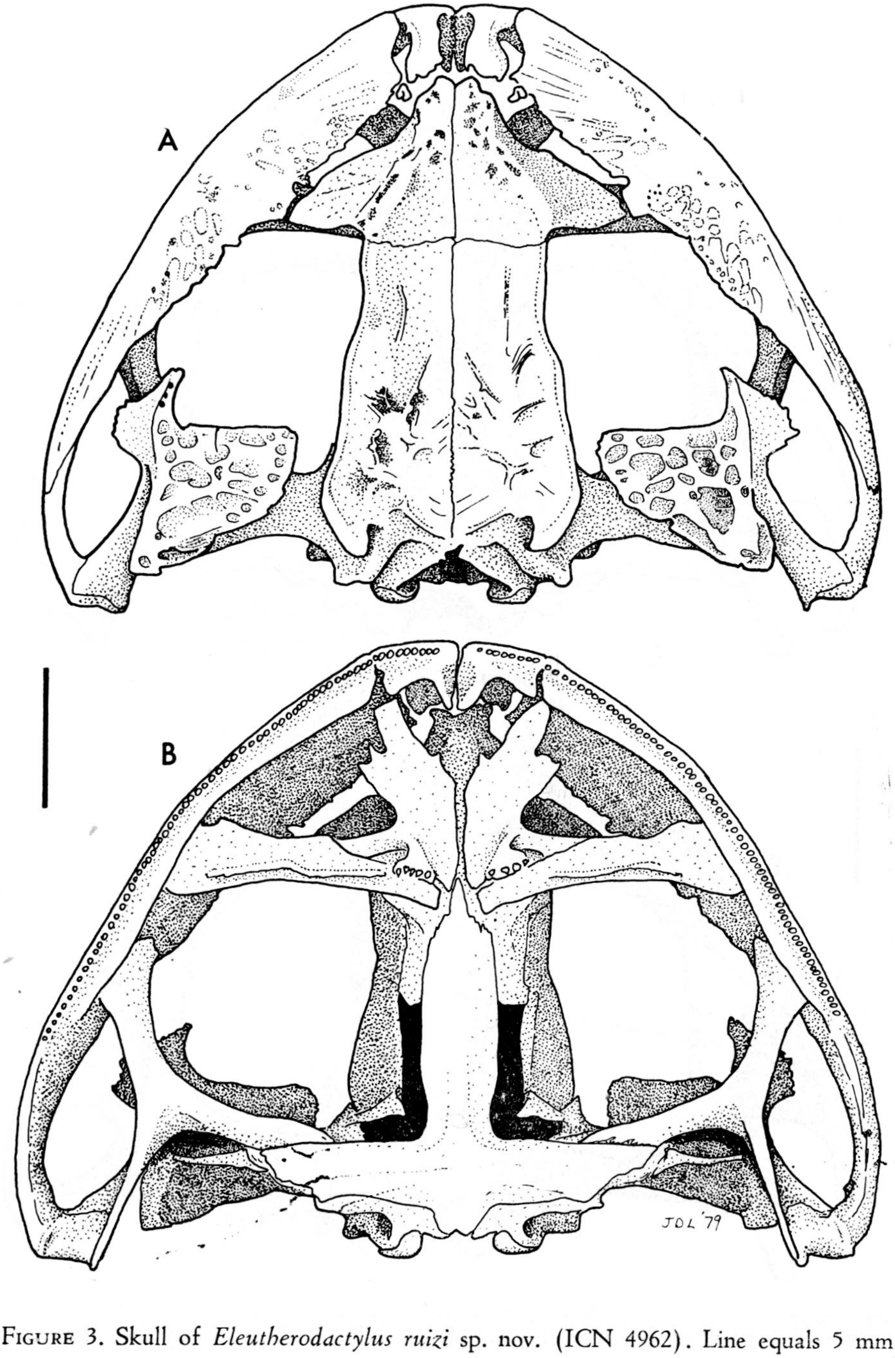

FIGURE 3. Skull of *Eleutherodactylus ruizi* sp. nov. (ICN 4962). Line equals 5 mm.

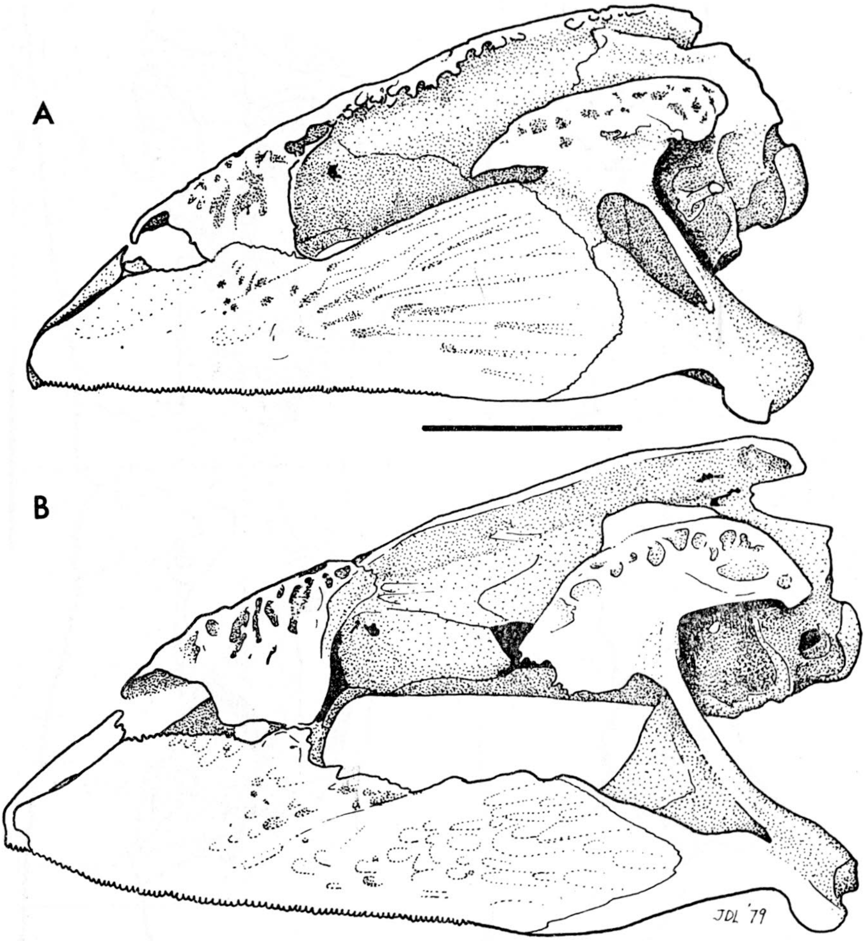

FIGURE 4. Lateral views of skulls of (A) *Eleutherodactylus ingeri* (ICN 2507) and (B) *E. ruizi* sp. nov. (ICN 4962). Line equals 5 mm.

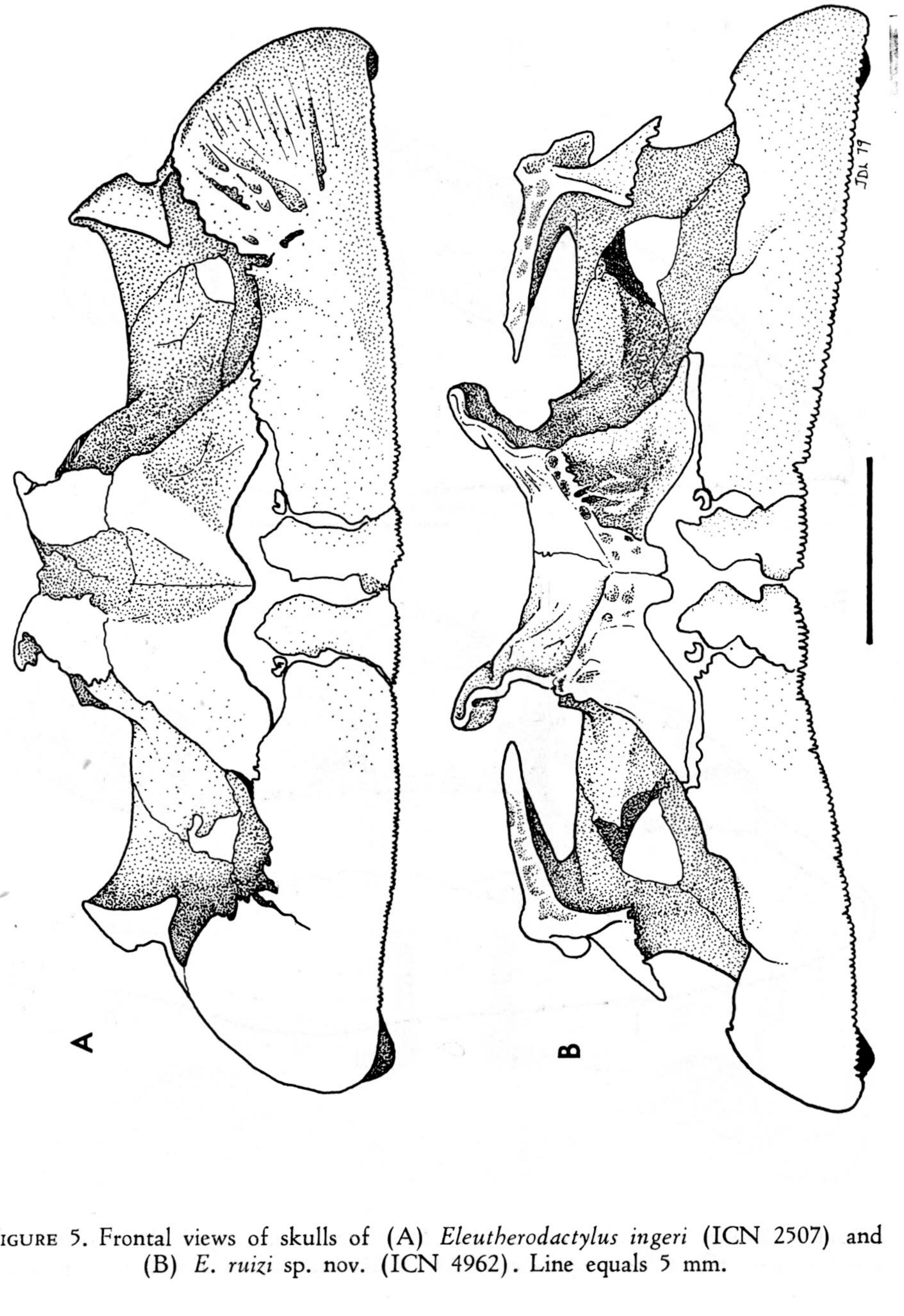

FIGURE 5. Frontal views of skulls of (A) *Eleutherodactylus ingeri* (ICN 2507) and (B) *E. ruizi* sp. nov. (ICN 4962). Line equals 5 mm.

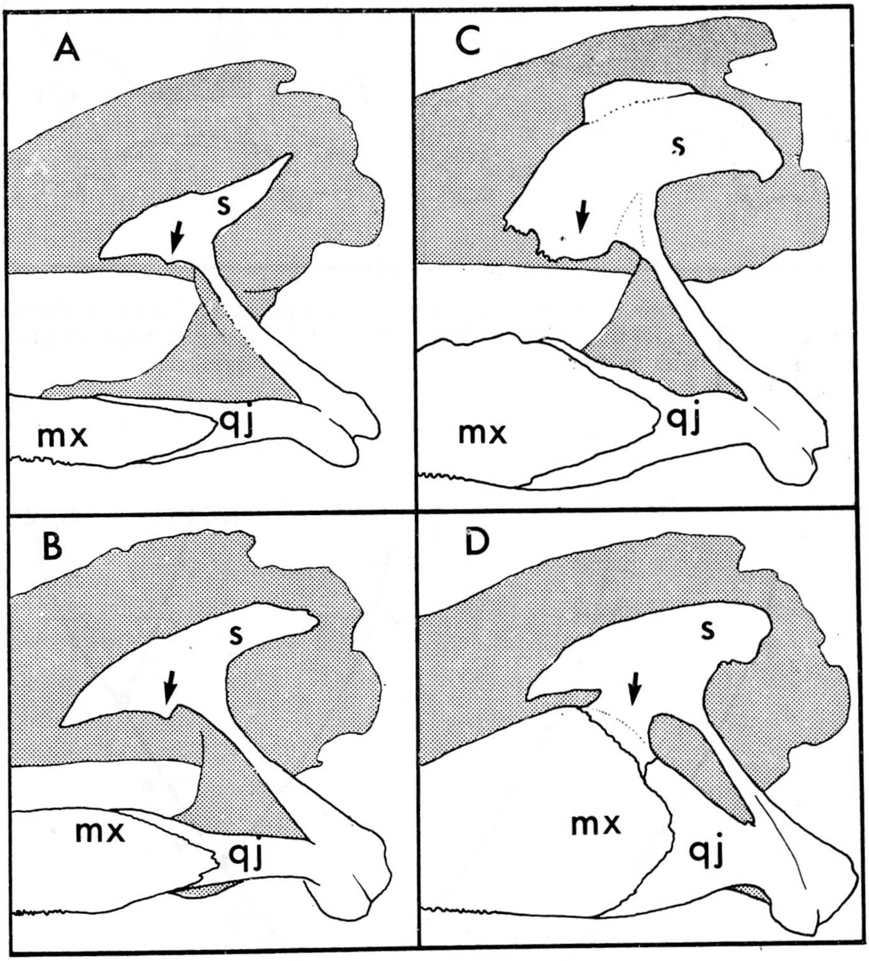

FIGURE 6. Lateral views of temporal regions of skulls of *Eleutherodactylus*, (A) *E. maussi*, UMMZ 113938; (B) *E. sulcatus*, KU 100355; (C) *E. ruizi* sp. nov., ICN 4962; (D) *E. ingeri*, ICN 2507. Arrows indicate presumed homologues, anteroventral flange of squamosal. mx (maxilla), qj (quadratojugal), s (squamosal).

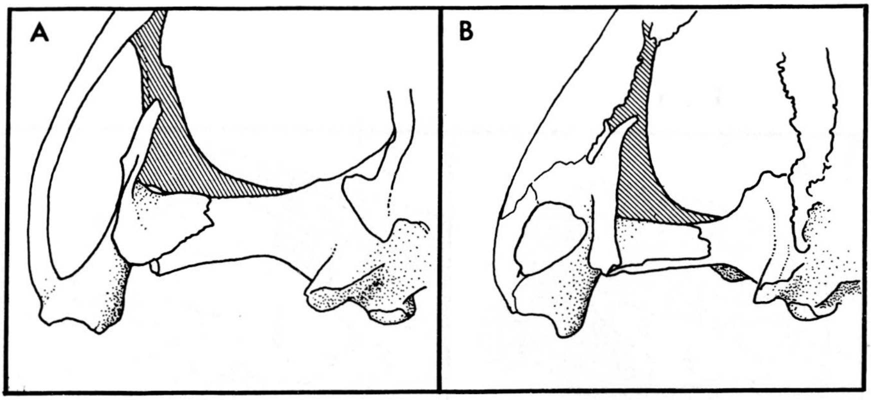

FIGURE 7. Dorsal view of posterolateral portions of skulls of (A) *Eleutherodactylus maussi*, UMMZ 113938, and (B) *E. ingeri*, ICN 2507, showing different character-states in median extension of otic plate of squamosal.

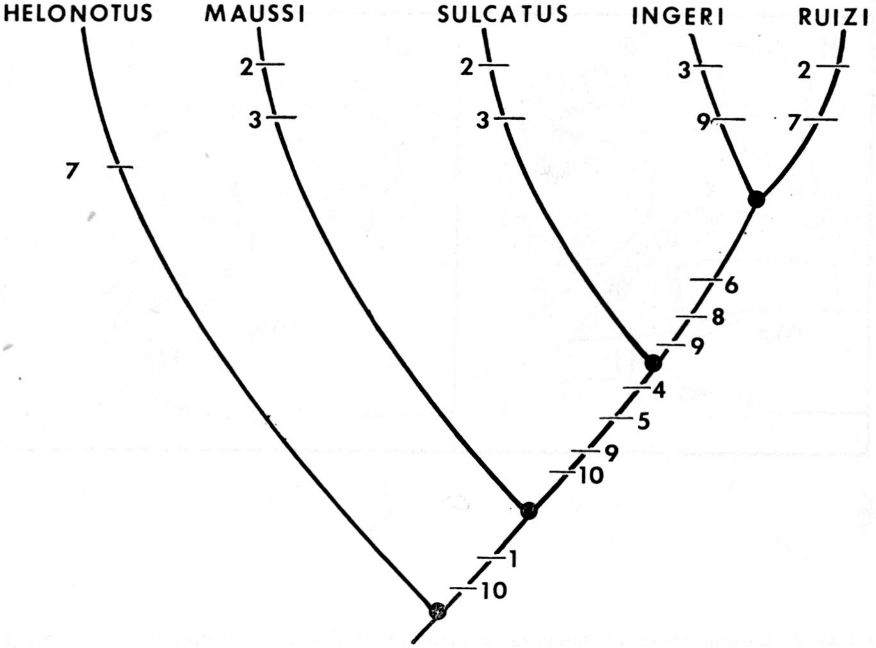
HELONOTUS
MAUSSI
SULCATUS
INGERI
RUIZI
7
2
3
2
3
3
9
2
7
6
8
9
4
5
9
10
1
10

FIGURE 8. Cladogram for the five species of the *sulcatus* group. Horizontal dashes and numbers refer to acquisitions of derived character-states (see Table 2).